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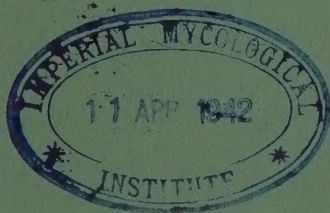
Interpreting Botanical Progress

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# THE BOTANICAL REVIEW

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## A REVIEW OF RESEARCHES CONCERNING FLORAL MORPHOLOGY

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In the following pages it is proposed to indicate the chief lines along which attempts have been made to solve the problems that have arisen in connection with the organisation of angiospermic reproductive structures. The treatment of the subject under three main headings is perhaps most likely to give a clear account of the work which has been done in the last few years: 1. the "old classical morphology"; 2. the "new morphology"; 3. "developmental morphology."

### 1. THE "OLD" MORPHOLOGY

It is a conventional and very generally accepted theory that the parts of a flower are the morphological equivalents of leaves (21); the implication is that they are transformed or metamorphosed leaves, an idea which is especially associated with the name of the German poet-philosopher, Goethe (28).<sup>1</sup>

As Asa Gray pointed out (29), the term "metamorphosis," as applied to the appendages of the aerial shoot of plants, is a *figurative* expression and is liable to mislead unless it is clearly understood that the "substance of the doctrine" is *unity of type*. That is to say, foliage leaves and floral organs may be of the same fundamental nature; but that does not necessarily imply that they are formed the one from the other.

The Goethean theory of metamorphosis is the underlying idea of the majority of the numerous researches into floral morphology from the time of its formulation until the present day. Two main kinds of evidence have been cited in its support, one from normally-developed flowers and the other from abnormal or teratological

<sup>1</sup> For accounts of the philosophical-botanical speculations of the latter part of the 18th and earlier part of the 19th centuries: 29, 54.



forms; and though the theory has become so deeply rooted and generally accepted that specific "proof" is no longer considered necessary, work is continued along these lines with two objects in view: first, that a more detailed knowledge of floral structure and organisation may be obtained; and secondly, that from this detailed knowledge a truly natural phylogenetic system of classification may ultimately be compiled (20).<sup>2</sup>

### 1. *Researches on normally-developed flowers*

For the moment, these may be considered as falling into two classes: (a) those which are concerned with the origin and development of the floral axis and of the various floral organs arising from it (organogenesis); (b) those which consider the structure, particularly the vascular anatomy, of the floral axis and its appendages (floral anatomy).

This classification is temporarily convenient since, in the past, such researches have been more or less independent.

#### (a) *Organogenetic studies*

The name chiefly associated with these is that of Payer (52). They have contributed to an understanding, not only of floral development, but also of comparative morphology and general floral plan as summed up, for example, in Eichler's "Blüthendiagramme" (24).

The original organogenetic observations were made directly on flower-buds from their earliest stages of development, observations involving great patience and extremely delicate manipulation. Modern researches on organogenesis have been facilitated by the use of the microtome; and while the older work was concerned simply with the composition of the flower and the origin and development of its parts, so far as these could be seen without sectioning, a new outlook is manifested in recent observations in that they are combined with other considerations, *e.g.*, cytological or anatomical.

Amongst morphological studies in which the development of the flower from the earliest stages is carried on through the cytological processes of the formation of pollen-grains and embryo-sacs to the

<sup>2</sup>It must be confessed that the newer researches do not seem to have greatly impressed the authors of the latest systematic works in which little or no mention is made of current ideas on the subject of Floral Morphology (53, 37; criticism of Rendle, 26).

production of embryo and endosperm, may be mentioned the work of Juliano and his collaborators in the Philippine Department of Agriculture (41-44) and that of Maheshwari and others at Agra, India (46, 47, 11). These careful researchers all add to the sum-total of detailed data which are of value in determining the relationships of the species dealt with.

(b) *Studies of Floral Anatomy*

The use of the microtome and the improvement of technique have made it possible to examine complete and uniformly orientated series of sections of floral structures in all stages of development from inception to maturity. In this way the form and order of appearance of floral appendages may be estimated and the origin and arrangement of their vascular system may be clearly apprehended. Not only must the structure be followed *from pedicel to apex of the flower* but observations of vasculature should be made from a *complete series of developmental stages in each case*; otherwise, deductions drawn from vascular anatomy may be misleading. That is to say, anatomical and organogenetic studies must be combined; and there is evidence in some of the later researches into Floral Morphology that this is being increasingly realised and that the old distinction between such studies—as, for example, in the work of Van Tieghem (98)—is being broken down.<sup>3</sup>

Anatomical studies of the flower date from the observations of Robert Brown who realised that more was needed than a knowledge of external form and of such features of venation as could be seen with the naked eye (6, p. 237). Brown's work was not followed up in England until Henslow, influenced by the work of Van Tieghem in France, published his observations on Floral Anatomy between the years 1876 and 1890 (34-36).<sup>4</sup>

<sup>3</sup> Arber (6) notes that since external shape and anatomical structure are two aspects of "form," i.e., they are the products of differential growth and development of the same fundamental mass of tissue, form, anatomy and ontogeny should be studied as an "indissoluble whole." While advocating this method as preferable to the purely analytical work (without subsequent re-integration) of so many English investigators, Arber considers that Troll (99), in Germany, has gone too far in a holistic and synthetic treatment of the plant, his view being that form is a unity which cannot be analysed. As Arber points out, the unreserved acceptance of this attitude, to the exclusion of analysis, would bring scientific work to a full stop.

<sup>4</sup> An historical sketch of anatomical studies of the flower is given by Grélot (31).

A new impetus was given to research in Floral Morphology in 1922-23; it is impossible to give anything like a comprehensive review of the many detailed studies which have now been carried out and an outline of their general scope must suffice, supplemented by the bibliography.

*Carpel Polymorphism.* At the British Association meeting at Hull, in 1922, E. R. Saunders exhibited abnormal gynaecea of the garden Stock in which evidences of a 4-carpellary constitution were apparent.<sup>5</sup> Influenced by these examples, she made an investigation of normal Crucifers which led her to uphold, as typical for the family, the 4-carpellary theory suggested primarily by Lindley in 1828 (45) and adopted by various subsequent observers, in opposition to the conventionally-accepted 2-carpellary view as explained in the text-books.<sup>6</sup>

Basing her contentions on the venation of Crucifer carpels and on the lines of dehiscence of mature fruits, and axiomatically stating that each original vascular cord passing from the floral axis to the gynaeceum represents the supply of a whole carpel (67, p. 128), Saunders has advanced the opinion that carpels are not uniform in type but that in the course of floral evolution *two main forms* have appeared: "(a) the valve or hollow type which is more or less extended laterally and, if fertile, bears the ovules either singly or in a single row on either margin; (b) the consolidated type which, if fertile, produces ovules either singly or in from one to several rows on each flank of the midrib" (68). This latter form of carpel, it is claimed, may consist simply of a solid vascularized column, or of a radial plate of tissue, or it may show extensions on either side of the midrib, forming the semi-solid, or pseudo-valve, type. This semi-solid form is regarded as variable in the amount of extension it may display;<sup>7</sup> presumably, also, extensions need not necessarily be symmetrical on both sides of

<sup>5</sup> Reference will be made to these in the next sub-section.

<sup>6</sup> Historical sketches of the various views regarding the constitution of the Crucifer gynaeceum and the nature of its characteristic dissepiment will be found in (22, 25, 57, 93).

<sup>7</sup> Cf. the cases of the typical legume and that of *Haematoxylon*, both regarded by Saunders as *bi-carpellary* in constitution, the former consisting of a "cardinal" solid and sterile carpel, + a "vexillary" semi-solid and fertile carpel; and the latter of two equal semi-solid carpels, one fertile and the other sterile: 61, pp. 143-4.



the midrib.<sup>8</sup> Thus, while Saunders has retained the conception of the carpel as fundamentally a leaf-like organ, she regards it as capable of undergoing the modifications of form indicated above and has summed up her theory in the term "Carpel Polymorphism."

With regard to the typical members of the Cruciferae, Saunders' view is as follows (57): The gynaeceum of the silique type is composed of two lateral valve-like sterile carpels and two median consolidated carpels, each bearing ovules on both sides of its vascular cord; the dissepiment dividing the ovary into two loculi is regarded as true carpellary tissue, actual parts of the two solid carpels and *not* a "false septum" formed by a secondary ingrowth of tissue. The stigmatic function is performed by the tips of the two reduced fertile carpels in most types (*e.g.*, Wallflower)—the difficulty seen by Saunders in the acceptance of a "commissural" stigma is thus removed; or it tends to be confined to the two sterile valves, as in the Stock, though this condition is rare (57); or again in exceptional cases, both sets of carpels may form stigmas. The gynaeceum of the silicula type (*e.g.*, Shepherd's Purse) is held to be formed on similar lines, except that from observations of venation Saunders regards the two fertile median carpels as semi-solid and the valve carpels as considerably reduced in extent (61).

Having based her theory upon observations of the Cruciferae, Saunders proceeded to investigate a very wide range of Dicotyledonous and Monocotyledonous families (58 *et seq.*). She now claims to have found Carpel Polymorphism exhibited almost universally amongst the Angiosperms, even in cases where, originally, she accepted monomorphism.<sup>9</sup> She regards polymorphism as having arisen in many instances in connection with a considerable reduction in carpel number; this is the case, for example, in the *Ranunculaceae*, *Rosaceae* and *Phytolaccaceae*. In various members of these families, there is a large number of carpels, all of the

<sup>8</sup> Cf. McL. Thompson (93, pp. 8-10), on the number of carpellary types which may be envisaged according to Saunders' theory.

<sup>9</sup> See, for example, *Melanthium*, at first accepted as possessing a gynaeceum of 3 fertile valve carpels (61) but now claimed as having a polymorphic gynaeceum of 3 fertile and 3 sterile carpels (63); *Papaveraceae*, formerly regarded as containing certain forms (*Platystigma* and *Platystemon*) with valve carpels only (61), now held to include nothing but polymorphic types (70).

*fertile valve* type; but in those members where the carpel number is reduced, polymorphism is believed to occur (71).

Saunders claims that her theory of Carpel Polymorphism explains satisfactorily various points of floral structure which have in the past appeared as anomalies or presented difficulties of interpretation. Some of the points thus "explained" are: the nature of "false septa" and the constitution of "commissural stigmas";<sup>10</sup> the "so-called" terminal carpel; the cause of obdiplostemony; the origin of parietal and free-central placentation; and the gynobasic style. She has certainly rendered a considerable service to the cause of Floral Morphology by stimulating long overdue anatomical enquiry into these various points, for her revolutionary treatment of the subject has raised much comment and criticism. Approval of her theory is expressed in a review of the "Classification of Flowering Plants," in which Rendle is taken to task for not giving due consideration to Saunders' explanations of obdiplostemony and other points (26); and Dowding is convinced of Carpel Polymorphism in *Arceuthobium americanum* (Loranthaceae) and in the Santalaceae (19); but it is evident that the theory has not commended itself to the greater number of workers in the field of Floral Morphology during the last 8 years.<sup>11</sup> There seems to be a general impression that problems have been raised where none existed, as in the case of the terminal carpel (*v. infra*, footnote 13); and that in many instances complicated explanations of comparatively simple matters have been invented to fit in with the theory as, for example, in the case of *Arachis hypogea* which is claimed to have from 10 to 12 carpels instead of 1 because, according to the rules of Carpel Polymorphism, the 10 or 12 longitudinally-running vascular strands of the ovary wall must each represent the supply of an individual carpel (93).

A measure of support for Saunders' original observations has come from Eames and Wilson (22) and from J. Dickson (18),

<sup>10</sup> For an anatomical defence of the usual explanation of the commissural stigma as made up of the united halves of normally placed stigmas, and a criticism of its necessarily complicated derivation if the polymorphism theory is to be generally applied: 21, pp. 184-5; Text-fig. 29.

<sup>11</sup> For criticism and repudiations of the theory as a whole, or in part, see, for example, 3, 4, 5, 6, 9, 12, 13-15, 18, 21, 22, 23, 40, 51, 81, 93; see also summary and comments by Barton-Wright (10). Saunders' replies to certain of these criticisms will be found in 62, 67, 75 and 77, where she re-states and extends her claims.



in so far that in the Cruciferae and certain other Rhoeadalean forms, these workers agree that the gynaecium is composed of carpels *differentiated* as "solid and fertile" and "valve and sterile" or, as Dickson prefers to term them, "*contracted* and fertile" and "*expanded* and sterile."<sup>12</sup> Their support is the more cogent in that they have added data from the vascular supply of the carpels; they hold that the carpel is fundamentally a 3-trace structure and that the vascular supply to the "solid" carpels, although greatly concentrated, is of the same nature and constitution as that to the "valve" carpels. They differ from Saunders in that they do not believe in the existence of the "semi-solid" carpel, as conceived by her.

So far, Eames and Wilson on the one hand and Dickson on the other are in agreement. Eames and Wilson, however, regard the solid carpels of the Crucifer gynaecium as having arisen by the phylogenetic elimination of the loculus of *closed* carpels, fused with one another across the centre of the gynaecium, and the dissepiment, as it now appears, to be the attenuated result of the contraction of these two carpels which are protected and partly enclosed by the other two, *open*, carpels (23). Dickson, on the other hand, has traced a series of forms through the Rhoeadales which may be interpreted as indicating the possibility that the gynaecium was ancestrally composed of *open* carpels only, fused margin by margin; in certain types a *lateral* contraction of alternate members is apparent, as in *Glaucium* and *Sanguinaria*, accompanied by restriction of ovule-bearing to the contracted carpels; contraction reaches its extreme expression in such forms as *Macleaya* and *Chelidonium*. The original conception of the dissepiment as an outgrowth of carpellary tissue appears to be justified by the course of events in *Glaucium* where, *after* formation of the ovules, a spongy embedding tissue grows out from the contracted fertile carpels, forming a loose "septum" across the ovary. In the Cruciferae the septum is of very early formation and it is of more coherent tissue than in *Glaucium*; but there is no reason to believe that it is anything but an extension of carpellary tissue, entirely comparable with that in *Glaucium*. In the Capparidaceae and

<sup>12</sup> J. Dickson's work is at the moment unpublished; a preliminary communication on the Papaveraceae has, however, been made by her to the Linnean Society, and the complete paper will shortly appear in the Society's Journal.

Fumariaceae the septum is not formed at all while in *Sanguinaria* slight traces of outgrowing tissue may appear at the base of the ovary.

Although, according to Dickson, carpel-differentiation seems to be characteristic of the Rhoeadales as a whole, the more primitive members of the *Papaveraceae*, *Platystemon*, *Platystigma* and *Romneya*, at least, possess carpels of uniform, undifferentiated type, the gynaecium of *Platystemon* showing, in construction, distinct similarities to that of certain *Ranunculaceae*.

Apart from the Rhoeadales, no example of carpel-differentiation has been found either by Eames and his collaborators or by Dickson though many families have now been investigated.

Special note should be made of the work of A. Arber in this connection. This author does not favour the theory of Carpel Polymorphism and, with regard to the interpretation of the Crucifer gynaecium, she holds that the anatomical basis of the 4-carpellary view does not stand examination; she believes that to ask how many carpels enter into its composition is an unanswerable question, for in this family the gynaecium "may never in the whole course of its history have passed through a stage in which it could be said to consist of distinguishable leaf members" (3). This latter statement is probably indisputable; but, as against the retention of the bi-carpellary theory "*as an instrument of description*," it may be suggested that the comparative work of Dickson on the *Papaveraceae* and other Rhoeadalean forms now indicates that the 4-carpellary theory would provide a better "*instrument*."

Since it does not appear that the theory of Carpel Polymorphism can be accepted as generally proven, it is not necessary here to examine categorically and in detail those points which it is held to explain; reference to a consideration of the main items from the view-points of Saunders and her opponents will be found in the works cited below.<sup>13</sup>

<sup>13</sup> Explanation of the "false septum" and "commissural stigmas" have already been noted in dealing with the Cruciferae. With regard to other points, the references are as follows:

(1) *The terminal carpel*. In the Leguminosae, for example, Saunders disposes of the "difficulty" by the theory of Carpel Polymorphism, according to which  $G=2$ , not 1, in this family (70, 63, 69, 71). Arber (2) and Eames (21) show how, by extreme reduction of apical tissue in determinate shoots, the terminal leaf-member, carpellary or otherwise, may become a reality.

(2) *Obdiplostemony*. Saunders has examined this in many families (61, 64, 73, 74, 75, 77) and concludes that it arises through Carpel Polymorphism.

*The Inferior Ovary.* As a result of her "Leaf-skin" studies and consideration of gynaecea, Saunders has expressed the view that the old term "epigynous," for those floral types with an "inferior" ovary, should be discarded in favour of "syngynous" (58, 59), or "syngonous," as it appears in later papers (63, 69, 74). The change of terminology is suggested on the grounds that the enclosing wall of the ovary is exclusively foliar, conclusions being drawn in the first place from certain Iridaceous forms and from *Begonia*. While it is true that in some of the Iridaceae and Amaryllidaceae (e.g., *Alstroemeria*) there are distinct evidences that the lower parts of all the whorls, perianth, androecium and gynaeceum, are conrescent,<sup>14</sup> it does not seem possible that this

In the case of *Pelargonium*, Bancroft and Dickson have shown that the cause of obdiplostemony is the carrying-out of the petal-stamen bundles by the petal midribs, so that petals + petal-stamens act as a single whorl (9); in the course of alternation of whorls, it follows that the carpels are developed opposite the petals. The same observation has been made in other families by these writers and also, in fact, by Saunders herself (77); in this paper Saunders claims that the carrying-out of the petal-stamen bundles by the petals allows space for the antepetalous carpels to develop loculi, while the antesepalous carpels remain solid, their development being hampered by the presence of the antesepalous stamens. This view would, of course, be reasonable, if Carpel Polymorphism could be accepted as a fact; but even so, it is difficult to see how Carpel Polymorphism could be the cause of obdiplostemony.

(3) *Free-central placentation.* In the Primulaceae, for example, Saunders holds that the free-central placenta is composed of fertile solid carpels, while sterile carpels form the wall of the ovary (75). In an as yet unpublished paper, Dickson has been able to show the connection between such 5-carpellary types as *Aquilegia* (Ranunculaceae), Geraniaceae, certain Silenoideae and the Primulaceae, a series in which no kind of carpel differentiation has been detected. The free-central placenta of the Primulaceae seems to be composed of fused carpel-margins ( $\pm$  residual axial tissue), detached from the wall of the ovary as they are in the Silenoideae, where, however, the detachment takes place ontogenetically. Cases of *parietal placentation* are explained by Saunders as in the Cruciferae (74); but that recourse to Carpel Polymorphism as an explanation is not universally necessary is shown, for example, by the case of *Platystigma* (18); reference should also be made to Bugnon's refutation of Carpel Polymorphism in *Drosera* (15).

(4) *The gynobasic style.* Under the Carpel Polymorphism theory, the gynobasic style is derived in various ways (59, 63). Work is being carried out at the Imperial Forestry Institute (Oxford) which indicates simpler derivations on the "monomorphic" view; this point must, however, be left until the evidence is complete.

<sup>14</sup> In a paper read before the British Association at Leicester in 1933 (38), Hyde produced evidence of "syngony" in the Campanuloideae. It may be noted that this paper is of interest in that Carpel Polymorphism and the conventional De Candolle view of the carpel are alike refuted in favour of yet another suggestion, namely, that the gynaeceum of the Campanuloideae is composed of one whorl of similar carpels, each enclosing a loculus and a bifid "ovuliphore," which arises ontogenetically from the floral axis and



is necessarily always the case. Bugnon has definitely repudiated the idea for *Begonia* where he holds that the wall of the ovary is *wholly axial*, from base to rim, and throughout its thickness (16). Moreover, instances of "floral cups" are demonstrable in certain perigynous Rosaceae which are axial in the lower part and foliar above (12, 39); and the possibility, in other perigynous forms, of cups which are axial from base to rim cannot be overlooked. From these latter types, the derivation of genuinely epigynous examples in which carpellary tissue is concrescent with the linear surface of the floral cup, is not unthinkable.

## 2. *Researches on abnormally-developed flowers*

Opinion is divided as to the value of abnormally-developed flowers in morphological interpretations. On the one hand are botanists who treat them as valueless;<sup>15</sup> on the other hand, there are many investigators who regard them as reversionary and, therefore, as "genealogical signposts," as Arber has termed them, to ancestral structures, or as indicators of morphological status.<sup>16</sup> A. P. De Candolle gave an impetus to the study of abnormalities from this point of view (61, 62) and he has had a considerable following (48, 102). Saunders, as already noted, was led to her conclusions concerning "polymorphism" of carpels in the Cruciferae by observation of teratological examples. Four-valved Stock fruits were found at the base of inflorescences where, she maintained, ontogeny might be expected to repeat phylogeny; these fruits were, therefore, claimed as reflecting an ancestral condition. Arber, however, points out that there is too great a tendency to choose, for discussion of this type, those abnormalities which fit in with preconceived ideas (4). She herself has found, at the base of inflorescences of *Nasturtium officinale*, flowers which have accessory flowers associated with each petal; to regard these as "ancestral" would be manifestly absurd. Further, as Arber notes,

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carpellary axil. (The writer of this article is indebted to Mr. Hyde for notes concerning his work, which, it is hoped, will be published in due course.)

<sup>15</sup> See, *e.g.*, the work of Gregoire who considers that the appearance of a leaf-like structure in the place of a stamen or carpel does not prove that stamens and carpels are modified leaves. He bases his objections to the conventional interpretation of such abnormalities on his observations that leaf-primordia and those of stamens and carpels are not identical (30).

<sup>16</sup> Cf. the work of Heinricher on proliferated *Primulas* which are held to demonstrate the origin of the ovules from leaf-tissue (32, 33).

most of the cases of so-called reversion which have been advanced against Dollo's "Law of Irreversibility in Evolution" (1), are meristic variations in which the number of parts is *higher* than normal; and there is no justification for the assumption that abnormalities of this kind are atavistic—they may equally well be futuristic.<sup>17</sup> Following Godron (27), she suggests that there may be a physiological interpretation of the abnormalities noted by Saunders and herself; for the lowermost (outermost) flowers of an inflorescence are free from the pressure which those towards the centre mutually exert upon one another; they are also more likely to be generously supplied with food-materials.

Arber, therefore, suggests a third attitude towards abnormally-developed flowers: scepticism with regard to their atavistic interpretation should be combined with recognition of their significance in the whole problem of causal morphology.

In connection with physiological interpretations of abnormally-developed flowers, reference may be made to the work of Schoute who regards meristic variation in general as "true variability," an expression of plasticity of the "flower-material," so to speak (79, 80).

A similar conclusion is reached by Müller, working especially on *Libertia*, an Iridaceous type in which none of the many variations is regarded as either reversionary or "futuristic" but as the result of environmental action on the plastic characters of the plant (49).

### 3. *Phylogenetic considerations*

Brief reference must be made under the heading of "The Old Morphology" to the very general belief that a relationship exists between the Angiosperms and the Cycadophyta (7, 8, 50, 100, 101). This belief is the outcome of a certain similarity of floral organisation in the Cycadeoids and the Angiosperms; and it has recently been considerably reinforced by the discovery of close resemblances in detail between the wood anatomy of the Cycadeoids and that of the Magnolias (101).

Comparisons have in the past been drawn between the microsporophylls of the Cycadeoids and the stamens of Angiosperms; and between the megasporophylls of *Cycas* and the carpels of

<sup>17</sup> Cf. also Worsdell, who believes that most cases of *simplification* are "progressive" rather than "reversionary" (102, Vol. 1, p. 5).

Angiosperms. The general conviction that these gymnospermic reproductive structures are obviously foliar has supported the accepted theory of the foliar nature of the angiospermic stamens and carpels.

The similarity of floral organisation noted above may, of course, be deceptive; and the comparisons between the spore-bearing organs of Angiosperms and Cycadophyta may be unwarranted. At the moment, however, it seems impossible to avoid the conclusion that some relationship, community of origin, at least, exists between the two groups. If, therefore, as H. H. Thomas suggests, the individual spore-bearing organs of the Cycadophyta are branch-systems rather than leaves, it seems that the classical morphology must be superseded in the case of the Angiosperms also, as explained in the following section.

## 2. THE "NEW" MORPHOLOGY

According to H. H. Thomas, the angiospermic flower is *not* the homologue of a vegetative bud (85); the clue to modern floral structures is to be found in the reproductive bodies of the Caytoniales, a Lower Jurassic group which was already angiospermic though manifestly of Pteridosperm affinities. The Caytoniales includes certain leaves and micro- and megasporangial structures which have not been found in organic connection but which, by association and from presumptive evidence provided by morphology and structure, are considered to belong to related forms (84). The leaves, *Sagenopteris*, may be regarded as generally angiospermous in type. The microsporangial structures, *Antholithus Arberi*, were pinnate in organisation, the apex and lateral branches showing dichotomous divisions, some of which were terminated by groups of "anthers," each with 4 longitudinal pollen-sacs. The megasporangial structures, *Gristhorpia* and *Caytonia*, were pinnate also; the branches were, however, not truly lateral, but arose from the upper surface of the axis; they consisted of shortly-stalked "ovaries" with basal, downwardly-directed "stigmas." There is no doubt that these "ovaries" were truly angiospermic, for each of them was a closed cupule, containing two rows of ovules produced along a line running from its stalk round its periphery; but whether the closed ovary of the Caytoniales bears any direct relation to the modern Angiosperm carpel is debatable.



In comparing the reproductive organs of the Caytoniales and of the Angiosperms, Thomas sets aside all preconceptions based upon the "old" morphology and proceeds to argue from new evidence, drawn from recent discoveries of primitive land-plants (Psilophytales), from researches on the Pteridophyta and from an increased knowledge of fossil Gymnosperms. This evidence, as Thomas notes, indicates that sterilisation of structures originally fertile is much more likely to have taken place than the metamorphosis of leaf-like structures into reproductive organs (84).

Starting, therefore, from *known forms* of fossil microsporangial branch-systems and postulating the operation of the processes of reduction and fusion, Thomas sees the product in the present-day *stamen* of the *Ranunculus* type, or in the *staminate flower* of *Populus* or *Juglans* (86);<sup>18</sup> and, from known forms of fossil megasporangial branches, he sees the same processes resulting in follicles of the *Caltha* type (84).

Some account of the suggested derivation of the follicle from the *Gristhorpia* type of megasporangial branch-system is necessary. From a study of venation, Thomas concludes that this apparently simple modern structure is fundamentally compound, consisting of an axial portion, and two ovule-bearing branches—such a structure, in fact, as might be produced by the reduction of a megasporangial branch of *Gristhorpia* to a short axis and a pair of ovaries (84). The dorsal vein of the follicle may represent that of the axis and the two marginal veins the ovule-bearing midribs of the ovaries. If the three segments of this reduced *Gristhorpia* became fused, a further reduction, involving the adjacent segments of the "ovaries," might take place, and the ovule-bearing midribs thus come to lie side by side. The stigmatic tissue, originally basal, extended upwards, reaching the apex of the now completely-evolved follicle (84).

Thomas seems to regard the penultimate tripartite structure with its three main veins (84) as a "palmate sporophyll"; this

<sup>18</sup> The derivation of the staminate flower of *Populus* is suggested from microsporangial structures such as those of the Upper Carboniferous *Crossotheca* and the Triassic *Pteruchus*. According to this view, the reproductive structures of *Ranunculus* and *Populus* are not strictly comparable and the polyphyletic origin of the angiospermic flower is thus suggested. Against this suggestion of polyphyletic origin, of course, is the uniformity of endosperm-formation in the Angiosperm embryo-sac (Cf. remarks by Ramsbottom in 86, p. 42).

terminology, it should be noted, suggests a measure of convergence between the new and the old morphologies, for Eames considers the carpel of Angiosperms to have been derived from a 3-lobed, 3-veined, palmate *leaf* (21). Under the circumstances, Thomas's term tends to convey an inaccurate impression of his derivation of the follicle. If, however, according to Arber's conclusions, axis and leaf are not to be treated as "discrete morphological entities" (2) distinctions between branch-systems, leaf-like branches and leaves finally disappear under the operation of "reduction and fusion" processes; and the differences between the derivation of the carpel from a "branch-system" and from a "leaf" are more superficial than fundamental. But the question really resolves itself into one of the *ultimate origin* of lateral appendages of the axis: they may be cladode megaphylls (modified branches) or microphylls, arising from the axis by enation. Bower's very cogent suggestion that the flower should be regarded as a strobilus bearing appendages very probably of *both* types, must be given due consideration; and against the *literal* interpretation of the theory of metamorphosis—which is still, unfortunately, only too prevailing<sup>19</sup>—must be set his dictum that "normally produced sporangia antedated any other constituent part of the flower upon which those sporangia are now borne" (86).

### 3. "DEVELOPMENTAL" MORPHOLOGY

An entirely new outlook on Floral Morphology is suggested by McL. Thompson (87-97) who, holding the opinion that the subject cannot be further advanced by an intensive study of mature structures (either recent or fossil), proposes instead a study of "developmental" morphology, in which it is held, as a fundamental principle, that number of floral parts, fertility, sterility and the development of the stigmatic function are matters of growth-physiology and of the chemistry of cell-nutrition (55).<sup>20</sup> Thompson believes that if angiospermic floral types are studied ontogenetically from their earliest stages to maturity, they may be their own interpreters, without recourse to any phylogentic considera-

<sup>19</sup> The idea of metamorphosis, it should be noted, was confused from the outset; Goethe, himself, used the term sometimes quite literally and at others in an idealistic sense.

<sup>20</sup> Developmental studies, based upon the same principles, are being pursued by Stirling in an endeavour to elucidate the phenomenon of heterostyly (82, 83).

tion other than the assumption of phyletic diminution of sporogenous tissue with accompanying reduction of apical growth (97).<sup>21</sup> He has, accordingly, made developmental studies of the Leguminosae (88-90, 93, 94), the Lecythidaceae (91) and the Scitamineae (95); and from evidences of advancing sterility in these families he has been led to a new theory of "the state of flowering known as angiospermy" (96, 97) in which he visualises the basis of the modern flower in a "sporogenous axis, devoid of obligate appendages."

Briefly, the evolution of the floral organs from this axis is suggested as follows: The lower part of the axis is sterile and ultimately produces sterile appendages, bracts, bracteoles and sepals. The base of its sporogenous tip is potentially microsporangial; from it emergences arise which ultimately become stamens; sterilisation of the lowermost microsporangial emergences results in petals or staminodes. The final positions of bracteoles, sepals, petals, staminodes and stamens are determined according to the maintenance of apical growth, or its replacement by toral growth. When toral growth becomes dominant over apical growth at an early stage and extends beneath the bracteoles and sepals, the maturing axis is cup-shaped and the "condition of the flower with inferior or semi-inferior ovary is initiated and is later attained if the dominance of toral growth is continued." The definition of "microsporangium" is closed by the production of emergences which are stigmatic and form "stylar components." The remaining axial surface which lines the cup is megasporangial; emergences from it ultimately become ovules.

Thus, in the case of types with semi-inferior or inferior ovaries, Thompson disposes of the conception of carpels entirely: the Scitamineae, for example, are described as "acarpous" (95).

With regard to types with superior ovaries, he holds that the only essential difference from those with inferior ovaries lies in the fact that, in their case, apical growth is maintained until the general form of the floral axis is determined. The whole surface tissue of the apex of the axis is potentially sporogenous and, after the cessation of stamen-production, there arise from it emergences

<sup>21</sup> The writer is greatly indebted to Professor McLean Thompson for permitting her to read his conclusion in MS. before the actual publication of his work.



which, by processes of initial enlargement by apical growth, local sterilisation and union, result in "ovuliferous phylloclades" (*not carpels*, according to the general conception); ovule-production becomes restricted, the placentae are thus defined and the ovules finally become enclosed, such gynaecial types as the legume and the follicle being produced (93, 94, 97). In these cases, Thompson holds that the emergences which eventually produce the "ovuliferous phylloclades" are potential stamens; their union marks the cessation of their initial apical growth; their development of stigmatisation is associated with their diversion from microspore-bearing and the initiation of the megasporangial phase. Thus, it appears to Thompson that there is an interplay and interdependence between the androecium and the gynaecium which cannot, therefore, "profitably be discussed apart in matters of development or descent." The conclusions which result from this view of the evolution of the angiospermic flower are that "a species with few carpels *per* flower has not descended from ancient forms with many carpels, some of which have been suppressed"; and "neither is the flower with superior ovary, as now known, considered primitive, nor is the flower with inferior ovary considered advanced. They express distinct states of flowering which may exist simultaneously in a single accepted affinity" (97).

It is interesting that his studies of developmental morphology have led Thompson to a theory of the strobiloid origin of the angiospermic flower which has certain resemblances to that suggested by Bower (*v. supra*) though it presents a simpler view of the origin of the various floral parts, in that, according to Thompson, they are all derived by "emergence" from the axis.

Attention should be drawn to certain of Clapham's comments on Thompson's work (17); this author notes that while it is "not difficult to agree that the carpel, growing for the most part by intercallary elongation *after* infolding, is no longer a leaf whatever its form in ancestral types," "there seems to be no strong reason, on grounds of structure and development, for calling it phylloclade rather than leaf." There truly is need, as Clapham says, for a revised morphological terminology—or at any rate, for a more meticulous use of existing terms.

Further, Clapham does not consider that the "acarpous" explanation of the Scitaminean gynaecium is legitimate: "the inferior

ovary is surely a derivative type in which the ancestral carpels have ceased to bear ovules and are represented only by the "stylar components"; and while, according to Clapham, the Scitaminean ovary is not now composed of carpels, "it cannot be maintained that it is ancestrally acarpous." The present writer would agree that all stages between epigyny and hypogyny are known and that the differences of condition seem to be determined by the distribution of growth after initiation of the carpels on the receptacle (16); but she does not hold it necessary to regard epigyny as having arisen in only one way (*v. supra*). Thompson's view of the existence of superior and inferior ovaries within single cycles of affinity is accepted as incontrovertible (*cf.*, *e.g.*, Hutchinson's new classification of the Liliaceae and Amaryllidaceae (37); but it is difficult to imagine that there is no serial and evolutionary connection between the two conditions.

It is regrettable that Thompson's studies of developmental morphology should not have included detailed observations of vascular anatomy; for while it is true, as he has said, that vascular anatomy is apt to be variable even within a species, experience (of the Primulaceae, for example) has indicated that if a sufficient amount of material is examined and if a sufficient number of developmental stages are followed serially, a fundamental plan of vasculature will be discovered which it does not seem possible to neglect in morphological determinations. As Arber admits, the *general scheme*, at least, of the floral vascular system "may have some value as indicating the broader trends of race history" (6); if that is so, while caution is undoubtedly necessary in interpreting floral anatomy, it is not desirable to set it aside entirely. Rather, it should be treated from the physiological standpoint Thompson himself advocates in dealing with developmental morphology as a whole and which Grélot, as long ago as 1897, realized as imperative (31). As he pointed out, in considering the structure of the bicarpellary Gamopetalae, floral parts show a great plasticity according to physiological needs and modification of the vascular tissue corresponds to modification of the ground tissue, the more so as the centre of the flower is approached. It is failure to realise the physiological aspect of vasculature, as Arber remarks (6) which has led Saunders to misinterpret the more strongly-developed vascular cords of the gynaeceum as the midribs of dis-

tinct carpels, for she has not considered the modification in venation of the carpels (as compared with foliage leaves) which has accompanied the shifting of function from midrib to margins.

In conclusion, then, it is evident that not only must considerations of angiospermic flower form and structure, both normal and teratological, be combined with developmental studies and checked by reference to palaeontological facts and to the reproductive structures of other living groups; they must be approached in relation to the problems of organic form and function as a whole; no line of investigation must be overlooked. The problems of organic form and function, however, as Arber remarks, await not only solution but even their full formulation.

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## GLOSSARY

*Enation*: outgrowth from the surface of an organ.

*Epigyny*: apparent attachment of sepals, petals or stamens to top of ovary; regarded as advanced stage.

*Free central placentation*: occurrence of ovules on a central axis is a one-loculed ovary, axis being unattached at its upper end.

$G=2$ : numeral indicates number of carpels composing gynoecium.

*Gynobasic*: arising from side or base of ovary.

*Hypogyny*: attachment of sepals, petals or stamens beneath ovary; more primitive than epigyny.

*Inferior ovary*: ovary of epigynous flower.

*Meristic*: pertaining to or divided into segments.

*Obdiplostemony*: condition wherein outer stamens stand opposite petals.

*Parietal placentation*: occurrence of ovules on peripheral wall of ovary.

## THE CYTOLOGICAL ANALYSIS OF SPECIES-HYBRIDS\*

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The cytological analyses of hybrids during the past decade have been of great value in determining the probable relationships and origin of many species of plants. The combination of cytological and genetic investigations has been so successful, especially in the analysis of cultivated plants, that the union between these sciences has been recognized as a permanent hybrid—"cytogenetics." A union between cytology and taxonomy also has been effected during recent years, but "cytotaxonomy" is not so well established.

A hybrid may be defined as an individual resulting from the union of unlike gametes. The gametic differences may involve gene mutation, chromosome morphology, chromosome number or various combinations of these variations. The parents may differ only in gene constitution in most varietal hybrids and apparently in certain species-hybrids. Most of these hybrids are fertile but genetic factors may cause meiotic irregularities and gametic sterility. Most hybrids derived from parents differing in chromosome structure or chromosome numbers are at least partially sterile.

### *Factors Involved in Chromosome Pairing*

In most intraspecific hybrids, the chromosomes behave as they do in the parental forms. The genetic evidence shows that there is a gene by gene pairing of homologous chromosomes at the prophase of the meiotic division. The cytological picture also shows, in favorable material, the pairing of similar chromomeres in the homologous chromosomes. The homologous chromosomes are usually held together until metaphase by one or several chiasmata, *i.e.*, an exchange of partners between paired threads or chromatids, of the bivalent chromosome. Although the chiasma frequency may be controlled by genetic and environmental factors, it can be used with caution as a rough index of chromosome homology. In most intraspecific hybrids, the meiotic divisions are regular and less than ten per cent of the pollen is aborted.

\* A glossary appears at the end of the article.



It has been assumed that the degree of chromosome pairing in species- or generic hybrids can be used as an index of chromosome homology and species relationships. But failure of chromosome pairing, or asynapsis, can be caused by genetic and environmental factors as well as by the lack of sufficient homology. All these factors must be considered in any interpretation of chromosome behavior in species-hybrids.

If two species can be crossed and produce a hybrid with normal somatic development, the parental genomes must be somewhat similar in essential genetic factors. In such hybrids, it seems improbable that differences in genetic constitution *per se* would produce sufficient lack of homology to cause a failure of chromosome pairing although it is possible that such factors may be involved.

Changes in chromosome structure are known to be an important factor in changing the homology of chromosomes in different individuals or species. Segmental interchange, inversions and loss or duplication of chromosome segments may change the chromosome structure of different species to such an extent that no two chromosomes in the species-hybrids are completely homologous. Slight changes would not inhibit regular pairing but the hybrid might be partially or completely sterile owing to segmental deficiency following random chromosome distribution at meiosis.

Genetic factors affecting chromosome morphology and chromosome pairing are known to occur in a number of species.<sup>1</sup> A single recessive character in *Matthiola incana* increases the length of the chromosomes at meiosis and decreases the degree of pairing. In *Zea*, a factor for "asynapsis" does not prevent pairing at prophase but chiasma formation is inhibited and pairing is reduced at metaphase. A similar condition is found in *Triticum*. Asynapsis, due to chromosome loss or to less definitely determined genetic factors, has been found in *Primula*, *Crepis*, *Datura*, *Viola*, *Nicotiana*, *Sorghum*, *Avena* and *Triticum*.

In the  $F_1$  of *Lolium*  $\times$  *Festuca*, Peto found regular chromosome pairing at meiosis but certain back-cross segregates showed irregular pairing. This behavior was attributed to segregation of factors limiting chiasma formation. The possible action of such complementary factors is also shown in species-hybrids of *Viola*, *Digitalis*,

<sup>1</sup> Huskins, 1932, and Darlington, 1932, Review and lit. cit.; Beadle, 1933; Sapehin, 1933.

*Chrysanthemum* and in certain generic hybrids in the *Gramineae*.

The nature of chiasma formation may be determined also by genetic factors. In *Allium fistulosa* the chiasmata are localized near the spindle fiber constriction, while in *Allium cepa* they are distributed at random. In the  $F_1$  hybrid between these two species the chiasma formation is at random. Back-cross segregates showed approximately equal numbers of plants with either random or localized chiasma (14).

Environmental conditions may play an important part in meiotic behavior of chromosomes. Either high or low temperature may cause a failure of chromosome pairing and the temperature extremes necessary to cause asynapsis are within the range which the plants occasionally might experience in nature. Irregularities in meiosis may be caused also by insects or virus diseases (20). Environmental factors causing meiotic irregularities are doubtless more effective in individuals with weak meiotic pairing, especially in hybrids.

The effect of genetic and environmental factors in chromosome pairing does make necessary some caution in interpreting chromosome relationships, based on chromosome behavior in species-hybrids. But this caution applies primarily to the negative aspects of the analysis. When chromosome pairing does occur, even though it may not occur consistently, there is usually good reason to believe that the pairing chromosomes are at least partially homologous. The conditions of pairing, even in many pure species, seem to be based on a delicate balance between chromosome development and the stage of meiotic development. These timing relationships may be so delicately adjusted that slight changes in genetic constitution, genic balances or environmental conditions may inhibit pairing of chromosomes which are completely homologous or at least sufficiently homologous to pair under favorable genetic and environmental conditions.

There are, however, certain types of chromosome association that are not dependent on chromosome homology. McClintock (24) finds in *Zea* an association of non-homologous chromosome segments, usually confined to cytologically unbalanced forms. The prophase association of non-homologous segments seems to be as intimate as homologous pairing but chiasmata are not formed and the non-homologous association rarely persists until diakinesis.

McClintock suggests that non-homologous prophase pairing is caused by a mechanism by which chromosomes start their pairing and by a force demanding 2 by 2 associations which can supersede that of homologous attraction when these forces are not working in unison. It is possible that some such factors may be involved in the pairing of non-homologous chromosomes in certain triploids and other cytologically unbalanced hybrids.

*Hybrids Between Species With the Same Chromosome Number  
Fertile Species-Hybrids*

Many hybrids between taxonomic species show regular chromosome pairing at meiosis and a high degree of fertility. The parental species in such hybrids presumably differ only in genetic constitution although minor structural changes may be involved. Regular pairing of the chromosomes at meiosis and a high degree of fertility have been found in certain species-hybrids of *Triticum*, *Ribes*, *Prunus*, *Fragaria*, *Salix*, *Vitis*, *Rhododendron*, *Platanus* and *Larix*.<sup>2</sup> In some cases, the  $F_1$  hybrids show a looser association of bivalent chromosomes than is found in the parental species. In hybrids between 14-chromosome wheat species, Aase notes an increase in the number of rod bivalents at the expense of the ring bivalents. Darlington has analyzed this hybrid in terms of chiasma frequency per bivalent and finds a frequency of 2 for the  $F_1$  as compared with 2.3 and 2.4 for the parents.

Hybrids between Asiatic or European species with American species are especially interesting because they afford an opportunity to study the effects of geographic isolation in species formation. Crosses between the European *Vitis vinifera* and the American *Vitis labrusca* are fertile and have produced many of our commercial varieties. Although *Platanus occidentalis* and *P. orientalis* must have been separated for thousands of generations, the  $F_1$  hybrid shows normal meiotic divisions and fertility. The  $F_1$  hybrid between Asiatic and European species of *Larix* is fertile and the chiasma frequency of the hybrid is as high as it is in the parental species. Such behavior would seem to indicate that such widely separated species have been differentiated without any

<sup>2</sup> Aase, 1930; Babcock and Navashin, 1930; Darlington, 1930, 1931; Hakansson, 1934; Meurman, 1928; Negrul, 1930; Percival, 1932; Sax, 1930, 1932, 1933; Yarnell, 1930.

fundamental genetic or structural changes in the chromosomes for very long periods of time. Certain species evidently differ only in minor genetic factors and maintain their identity only by isolation.

Crosses between different genera also may produce fertile hybrids.<sup>3</sup> The hybrid between the closely related genera *Sorbus* and *Aronia* shows normal chromosome pairing at meiosis and a high degree of fertility. *Zea mays* crossed with certain varieties of *Euchlaena mexicana* produces an  $F_1$  which has normal meiotic divisions and is fertile. Peto found regular pairing of the meiotic chromosomes in a cross between *Lolium* and *Festuca* although there was some evidence of structural hybridity.

### *Sterile Species-Hybrids*

In certain species-hybrids there is regular chromosome pairing at meiosis but the hybrid is partially or completely sterile. Such sterile species-hybrids have been found in *Primula*, *Aquilegia*, *Pisum*, *Philadelphus* and *Campsis*.<sup>4</sup> In the  $F_1$  of *Primula floribunda*  $\times$  *P. verticillata* the nine chromosomes from each parent appear to pair regularly but little good pollen is formed. More than half of the pollen is sterile in the species-hybrids of *Pisum* and Lutkov attributes this sterility to unfavorable genic combinations following the random distribution of the parental chromosomes to the microspores. The writer suggested that the partial sterility in the species-hybrid of *Campsis* might be caused by structural hybridity involving only small chromosome segments. Random distribution of the chromosomes would result in deficiencies of a chromosome segment in certain microspores with corresponding pollen sterility.

Irregular meiotic divisions and pollen sterility are characteristic features of most species-hybrids. Even when the parental species have the same number of chromosomes there is often considerable irregularity in the meiotic divisions in the hybrids. Such species-hybrids have been described in *Nicotiana*, *Crepis*, *Ribes*, *Rosa*, *Brassica*, *Viola*, *Aegilops*, *Gossypium* and in several hybrids.<sup>5</sup> In

<sup>3</sup> Beadle, 1932; Longley, 1924; Peto, 1934; Sax, 1931.

<sup>4</sup> Lutkov, 1930; Newton and Pellew, 1929; Skalinska, 1932; Sax, 1933.

<sup>5</sup> Babcock and Navashin, 1930; Clausen, 1931; Erlanson, 1929; Goodspeed, 1934; Karpechenko, 1927; Morinaga, 1931; Meurman, 1928; Percival, 1932; Webber, 1934.



the genus *Nicotiana* different crosses between 12-chromosome species show almost all degrees of chromosome pairing. The hybrid between *N. paniculata* and *N. Cavanillesii* shows very little chromosome pairing and the few bivalents formed are loosely paired. On the other hand, *N. paniculata* crossed with *N. solanifolia* produces an  $F_1$  hybrid with nearly normal pairing at meiosis and the bivalents are usually as closely paired as they are in the parental species. Other species-hybrids show an intermediate condition with much variability in the amount of chromosome conjugation. Goodspeed concludes that the degree of chromosome pairing in species-hybrids is an index of genetic relationships in *Nicotiana*.

In all species-hybrids with partial pairing of chromosomes there is great variability in the amount of pairing in different pollen mother cells. This variation is especially striking in crosses between 10-chromosome *Brassica* species where the number of bivalents may range from 1 to 9. Chromosome pairing in partially sterile species-hybrids also seems to be much more dependent on environmental conditions than is the case in pure species. The greater protection afforded the developing female gametophytes may account for the fact that the percentage of fertility is greater for the egg cells than for the pollen in many species-hybrids.

In these species-hybrids with failure of chromosome pairing, there is more or less gametic sterility caused by irregular distribution of the univalent chromosomes. These unpaired chromosomes may pass at random to the poles with the dividing bivalents, in which case they divide at the second meiotic division, or they may become oriented on the metaphase plate and divide after the division of the bivalents and pass undivided to one pole or the other at the second division. In either case, some of the univalents often do not reach the poles in time to be incorporated in the daughter nuclei and, consequently, the microspores are deficient in chromosomes necessary for normal development. When no pairing occurs, the univalents, in rare cases, may not complete the first meiotic division, but divide in the second; or they may divide equationally in both divisions. In either case, diploid gametes may be produced which contain the complete haploid complement of chromosomes from each parent. The union of two such functional

gametes is one means of producing the fertile constant species-hybrids to be described later.

Species-hybrids may be so sterile that no gametes are produced.<sup>6</sup> In a *Philadelphus* hybrid between diploid species, the anther contents disintegrate before the meiotic divisions are initiated. East finds a similar condition in certain male sterile segregates in a *Nicotiana* hybrid. The hybrid between *Mahonia* and *Berberis* has been grown in European and American botanic gardens for more than fifty years but it has never been known to produce flowers, even though the  $F_1$  plant is vigorous. Dermen finds 14 pairs of chromosomes in each of the parental species and 28 chromosomes in the somatic cells of the hybrid. Still greater incompatibility is shown in both varietal and species-hybrids where the embryo may die at an early stage of development.

#### *Hybrids Involving Differences in Chromosome Structure*

Structural hybrids are those in which the parental genomes differ in chromosome structure caused by rearrangement of chromosome segments. It is evident in many genera that species differ in chromosome morphology even though the chromosome numbers are the same. There is also good evidence that structural differences may be involved, even when the genomes of different species appear to be similar in chromosome structure.

The most easily recognized types of structural differences are found in individuals heterozygous for reciprocal translocations of large segments. If Aa and Bb are two non-homologous chromosomes, then segmental interchange will give rise to two new types of chromosomes, Ab and Ba. In individuals heterozygous for the two types of chromosomes, the homologous segments pair at meiosis to produce an association of four chromosomes. At metaphase, these chromosomes usually are associated by terminal chiasmata to form a ring or chain of four chromosomes, no two of which are completely homologous. In certain species, the adjacent chromosomes usually pass to opposite poles at meiosis but in most cases adjacent chromosomes pass to the same pole or to opposite poles at random. When adjacent chromosomes pass to the same pole, the gamete is deficient for a chromosome segment and may not be functional. For example, in the chain Aa-aB-Bb-bA, the

<sup>6</sup> Dermen, 1931; Hollingshead, 1930; McCay, 1933; Sax, 1931.

segregation of Aa-aB and Bb-bA to opposite poles will produce microspores deficient for segments b or a.

Segmental interchange has been found in *Datura*, *Zea*, *Pisum*, *Campanula*, *Rhoeo*, *Tradescantia*, *Aucuba*, *Oenothera*, *Godeitia*, *Clarkia*, *Hypericum*<sup>7</sup> and other genera. Complete rings involving all chromosomes are found in certain species of *Oenothera* and *Hypericum* and in *Rhoeo*. In these cases, the ring formation is perpetuated by a balanced lethal system which prevents the production of individuals homozygous for chromosome structure. In *Oenothera* these structural hybrids are also heterozygous in genetic constitution but segregates occasionally occur when further interchange occurs between chromosomes of opposite complexes. In other cases, however, different strains or different species may be homozygous for segmental interchange chromosomes and the rings are formed only when crossing brings together different structural genoms.

Different species may differ in chromosome structure even though the differences do not produce the rings and chains in the  $F_1$  hybrids. An extreme type of structural differentiation has been found in a cross between *Crepis divaricata* ( $n=4$ ) and *C. dioscorides* ( $n=4$ ). At meiosis there is variable pairing in  $F_1$  with the production of 0-4 bivalents (29). Some of the bivalents separate with difficulty; chromatids often break; fragments are produced; and occasionally a chromosome is found with two fiber attachments. Müntzing attributes this behavior to pairing of similar segments in structurally different chromosomes followed by crossing-over in the homologous segments. Similar observations have been made in species-hybrids of *Paeonia* by Stebbins (unpublished). If the parental genoms differ only in small or interstitial chromosome segments, the pairing may be regular, but random distribution of bivalents might produce segmental deficiencies which would cause partial sterility. There is some evidence of such behavior in certain partially or completely sterile species-hybrids. The indirect evidence from chromosome structure in related species supports the hypothesis that structural changes have been an important factor in the origin and differentiation of certain species (4).

<sup>7</sup> Sharp, 1934, lit. cit.

*Hybrids Between Varieties or Species With Different  
Chromosome Numbers*

Hybrids involving differences in the chromosome numbers of the parental gametes are of two kinds, autopolyploids and allopolyploids. In the first type, one or both of the parental gametes contain two or more sets of chromosomes which are essentially similar in genetic constitution and morphology. In the allopolyploid hybrids, the polyploid parent or parents produce gametes containing two or more sets of chromosomes which are only remotely homologous. Such allopolyploid numerical hybrids always involve genetic differences, and in some cases structural differences, in the parental chromosomes. It is obviously difficult to classify all numerical hybrids into these two types because intermediate conditions are found in some hybrids.

*Autopolyploid Hybrids*

The simplest polyploid hybrids are varietal triploids, derived from the union of a normal haploid gamete and an exceptional diploid gamete produced by a diploid plant. Crosses between diploids and tetraploids belonging to the same, or to closely related, species also give rise to triploids with three sets of chromosomes or genomes which are essentially identical. Autotriploids have been found in many different genera of plants. The cytological work on such triploids has been reviewed in a recent paper by East (13). Since all three genomes are identical or very similar in such triploids, one might expect pairing between the homologous chromosomes to form trivalents. Complete sets of trivalent chromosomes are common in triploid *Datura*, *Canna* and *Hyacinthus*, and trivalents are usually formed in *Lycopersicum* and *Zea*. Varying numbers of bivalents, univalents and trivalents are found in triploid *Prunus*, *Petunia*, *Pyrus* and *Tradescantia* but the total number of bivalent and trivalent chromosomes is usually equal to the basic chromosome number for the genus. Trivalent association is partially dependent on chiasma frequency. If the chiasma frequency is low, only two of the three chromosomes may pair, leaving the third chromosome as a univalent. In all cases, the chiasma frequency is greater in the triploid than in the diploid.

At the reduction division of the triploid, there is a tendency for the chromosomes of two genomes to pass to opposite poles and for



a random distribution of the chromosomes of the third genom, whether they are present as univalents or combined as trivalents. At the second meiotic division all chromosomes divide and the microspores receive from  $1n$  to  $2n$  chromosomes, the frequencies approaching those expected in a normal frequency distribution. Usually, however, there is some irregularity in division and some chromosomes do not reach the poles in time to become incorporated in the daughter nuclei. If a microspore receives a complete set of chromosomes or a complete genom plus additional chromosomes, the microspore usually develops and produces a functional pollen grain; but a microspore deficient for any one chromosome of the genom usually does not undergo nuclear division and sterile pollen is produced. According to King, most of the pollen sterility in triploid *Tradescantia* can be attributed to chromosome deficiency.

When "triploids" are crossed with diploids, there is usually a great excess of segregates with  $2n$  or  $2n + 1$  or  $2$  chromosomes, especially if the triploid is used as the pollen parent. The aneuploid segregates with intermediate chromosomes have a lower viability and fertility and tend to be eliminated in natural selection. The rapid elimination of the aneuploid types can be attributed to selective fertilization, selective elimination of zygotes and lack of favorable chromosome balance in aneuploid segregates.

An exceptional type of chromosome pairing is found in certain triploids of *Rubus*, *Fragaria* and *Nicotiana*. In *Fragaria*, for example, Yarnell finds that the 21 chromosomes of the triploid form 10 pairs of bivalents plus a univalent, or 9 pairs plus a trivalent, at the first meiotic division. East also finds some evidence of non-homologous pairing in a triploid of *Nicotiana Tabacum*.

More complex types of autopolyploid hybrids have been described in several genera. In a hybrid between a diploid species of *Prunus* and a hexaploid species, Darlington found 16 pairs of chromosomes. The 8 chromosomes contributed by the diploid, pair with 8 chromosomes from the hexaploid, and the two remaining genoms of the hexaploid pair with each other. Somewhat similar cases were found in a *Papaver* hybrid by Ljungdahl and in a *Betula* hybrid by Helms and Jørgensen. A somewhat more complex case in *Chrysanthemum* is described by Shimotomai. In a cross between an octoploid and a tetraploid species, the  $F_1$  had

27 bivalents, attributed to pairing within parental genomes (18 + 18) 1 (9 + 9).

Pairing between genomes from one parent only has been found in a species-hybrid of *Crepis* by Collins and Mann and in a *Zea-Tripsacum* cross by Mengelsdorf and Reeves. The two genomes contributed by the tetraploid parent pair with each other, leaving the haploid contribution from the other parent unpaired. Partial or variable pairing among the chromosomes contributed by one of the parents is found in other species-hybrids. A detailed summary of the various types of polyploid hybrids is presented in tabular form in Darlington's "Recent advances in cytology."

### *Allopolyploids*

Typical examples of allopolyploidy are found in species-hybrids of *Triticum*, *Nicotiana*, *Fragaria*, *Gossypium* and other genera. In crosses between Emmer wheats with 14 pairs of chromosomes and Vulgare wheats with 21 pairs of chromosomes, the  $F_1$  meiosis shows 14 bivalents and 7 univalents. The bivalents divide regularly but the univalents lag behind and divide equationally as the bivalent homologues reach the pole. At the second meiotic division the 14 bivalent homologues divide equationally and the univalents are segregated at random, without dividing, to either pole. Occasionally, univalents are lost at either the first or second meiotic division. The gametes produced contain from 14 to 21 chromosomes. About 20 per cent of the pollen grains are aborted but nearly all the egg cells seem to be functional. In  $F_2$  and subsequent generations, segregates with intermediate chromosome numbers are eliminated. The segregates with 14 pairs of chromosomes resemble the Emmer parent, while the 21-chromosome segregates resemble the Vulgare parent. *Aegilops cylindrica* crossed with Vulgare wheats produces an  $F_1$  with 7 bivalents but when crossed with the Emmer wheats, there is no pairing in  $F_1$ . The analysis of these and other hybrids indicates that the Vulgare wheats contain three different genomes of 7 chromosomes each.<sup>8</sup>

Crosses between certain 12- and 14-chromosome species of *Nicotiana* also indicate that allopolyploidy is a factor in species differentiation in this genus.<sup>9</sup> *Nicotiana sylvestris* ( $n=12$ )

<sup>8</sup> Sharp, 1934, pp. 366, lit. cit.

<sup>9</sup> Goodspeed, 1934, lit. cit.

crossed with *N. tomentosa* ( $n=12$ ) produces an  $F_1$  with no pairing at meiosis but either of these species crossed with *N. Tabacum* ( $n=24$ ) produces a hybrid with 12 univalents and 12 bivalents at meiosis. Clausen concludes that the *Tabacum* genom consists of two subgenoms, one homologous with the *N. sylvestris* genom and the other with the *tomentosa* genom. This hypothesis is verified by further analysis of a triplex hybrid. Kostoff crossed *N. sylvestris* with a form of *N. tomentosa* (Rusbyi, according to Kostoff, but *tomentosiformis*, according to Goodspeed) and obtained no pairing in  $F_1$ . A few diploid pollen grains were produced which functioned in the cross between the  $F_1$  and *N. Tabacum*. In the triple hybrid obtained, there were 24 bivalents at meiosis, produced by the pairing of the two genoms from the diploid pollen grain and the corresponding genoms of *Tabacum*.

#### *Amphidiploid Hybrids*

Amphidiploid hybrids are derived from sterile species or generic hybrids by doubling of the chromosome number. In the sterile hybrid the chromosomes may not pair, or if bivalents are regularly formed, the segregation of parental chromosomes produces unviable combinations. In the amphidiploid, each parental genom is duplicated and the chromosomes of similar genoms pair together. In most cases, bivalent pairing occurs; each gamete receives a complete genom of each parental type; fertility is restored; and the hybrids breed true to type. Chromosome doubling may occur either in the soma or in the gametes of the original hybrid.

In 1917, Winge suggested that many of the polyploid species in nature were allopolyploids derived from species-hybrids. This suggestion has been amply confirmed during the past ten years. The first complete analysis of an amphidiploid hybrid was made by Clausen and Goodspeed in 1925. *Nicotiana Tabacum* ( $n=24$ ) crossed with *N. glutinosa* ( $n=12$ ) usually produces an  $F_1$  with irregular chromosome pairing and a high degree of sterility but a few  $F_1$  plants were obtained which were fairly fertile and bred true. These plants had 36 pairs of chromosomes at meiosis, 24 pairs contributed by one parent and 12 by the other. The origin of this constant hybrid, *N. digluta*, was attributed to chromosome doubling in the egg cell. The amphidiploid hybrid *Primula Kewensis* originated as a bud sport from a partially sterile species-

hybrid. The generic hybrid *Raphanobrassica* was produced by chromosome doubling in  $F_1$  gametes. In the cross between *Raphanus* and *Brassica*, Karpechenko found that the 9 chromosomes contributed by each parent failed to pair in  $F_1$ , but some diploid gametes were formed. The union of such gametes produced plants with 18 pairs of chromosomes which were fertile and constant.

Amphidiploid hybrids have been described in many other genera including *Rosa*, *Solanum*, *Digitalis*, *Aesculus*, *Triticum*, *Saxifrage*, *Spartina*, *Brassica*, *Galeopsis*, *Phleum*, *Viola*, *Crepis*, *Salix*, *Fragaria* and *Gossypium*.<sup>10</sup>

In several cases, it has been shown that Linnaean species are amphidiploids and the parental species have been identified. In fact, Müntzing (1930) has been able to synthesize *Galeopsis tetrahit*, a tetraploid species, by crossing two diploid species, *pubescens* and *speciosa*. The  $F_1$  was almost completely sterile but did produce a triploid  $F_2$  plant which, when crossed with one of the parents, produced a tetraploid plant indistinguishable from *G. tetrahit*. *Spartina Townsendii* and *Pentstemon neotericus* are other examples of amphidiploids in nature whose origin is well established by cytological analysis.

Many of the experimentally produced amphidiploids are fertile but some of them are more or less sterile. The degree of fertility seems to be correlated with the degree of differentiation of the genomes of the parental species. If only remote homologies exist in the two genomes, pairing is restricted to homologous chromosomes from each genom, only bivalents are formed and the hybrid is fertile; but if the parental genomes are not so completely differentiated, then multivalent chromosome associations or random pairing between the chromosomes from different genomes, will cause irregularities in meiosis leading to partial sterility. Thus, there is generally a negative correlation between the fertility of the diploid  $F_1$  and the amphidiploid hybrid but sterility may be caused by complementary genetic factors in some cases.

There is other less direct evidence which indicates that many species, genera and even larger taxonomic units have originated

<sup>10</sup> Lit. cit. Winge, 1932; Darlington, 1932; Sharp, 1934. More recent work on *Gossypium* by Skorsted, 1934, and Webber, 1934; on *Pentstemon* by Clausen, 1933; and *Erophola* by Winge, 1933.



as amphidiploids. An outstanding example is found in a subfamily of the *Rosaceae*.<sup>11</sup> All genera of the *Pomoideae* have a basic chromosome number of 17 but the basic number for most other genera of the *Rosaceae* is 7 or 8. In diploid genera of the *Pomoideae* there is frequently considerable "secondary pairing" of chromosomes, suggesting remote homologies within the basic genom of 17 chromosomes. The genetic behavior of *Malus* is complex. These various lines of evidence suggest that the *Pomoideae* are allopolyploids, derived from remote ancestral types with 8 and 9 chromosomes, which in turn may have been derived from species or genera with 7 pairs of chromosomes.

Lawrence (21) finds in many species some secondary association of bivalents at meiosis, suggesting some homology within the chromosomes of each parental complement, sufficient to cause some attraction but not enough to cause chiasma formation and true multivalent pairing. Such secondary pairing, together with a comparison of basic numbers in related genera, may be of value in determining the original basic chromosome number in many genera.

#### *Chromosome Behavior in Hybrids as an Index of Species Relationships*

The cytological analysis of species-hybrids has been of value in determining the relationships and origin of many species of plants. Species which produce hybrids with regular meiotic pairing and normal fertility appear to be differentiated primarily by differentiation of genetic factors. Such species retain their identity only by geographic or physiological isolation.

Partial and variable pairing in diploid species-hybrids can be attributed to structural differences in the parental genomes or to the action of different genetic factors which inhibit chromosome pairing. Structural changes in the chromosomes seem to be an important factor in species differentiation. Such structural changes may in themselves produce morphological variation; and since these changes often inhibit the production of fertile hybrids, they may provide the necessary isolation for the development of diverse species by further accumulation of character differences by gene mutations. Structural changes in chromosomes have been an

<sup>11</sup> Moffett, 1933; Sax, 1933.

important factor in species differentiation in *Crepis* and other genera and seem to be associated with genetic differentiation in the Conifers.

Autopolyploidy may be a factor in species differentiation either as a direct result of chromosome duplication or by the partial isolation of the polyploid from the diploid, permitting independent development of specific differences. The allopolyploids, however, are of much greater importance in the origin of species and genera. Crossing of distinct species of plants followed by chromosome doubling is known to occur in nature and has occurred frequently under experimental conditions during the past ten years. It is of interest to note that many of our cultivated plants are of known or supposed allopolyploid origin. These include wheat, oats, cotton, apples, pears and tobacco. Allopolyploidy has been an important factor in the origin of species and of even larger taxonomic units. Anderson (2) suggests that certain angiosperms may have been derived from species of primitive gymnosperms by allopolyploidy.

Gene mutation, structural changes of the chromosomes, hybridization and polyploidy have been involved in the origin and evolution of species of plants. Cytological analyses of species and species-hybrids have shown which of these factors, or combination of factors, have been responsible for species differentiation in many different genera.

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## GLOSSARY

*Selected by the editors from Darlington's "Recent Advances in Cytology"*

*Aneuploid*, having an uneven multiple of the basic number of chromosomes through purely numerical aberration—an unbalanced polyploid.

*Balance*, the condition in which the genes are adjusted in proportions which give satisfactory and normal development of the organism.

*Basic Number*, the supposed number of chromosomes found in the gametes of a diploid ancestor of a polyploid.

*Bivalent* (v. Univalent).

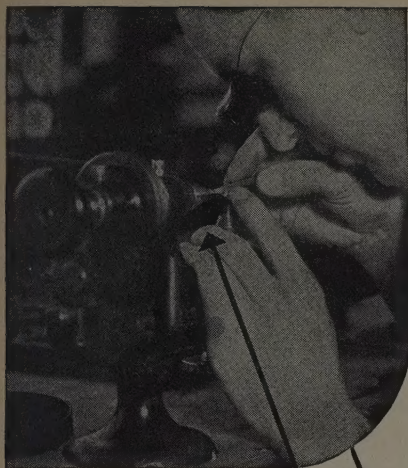
*Chiasma*, -*ta*, an exchange of partners in a system of paired chromatids.

*Chromatid*, a half chromosome between early prophase and metaphase of mitosis and between diplotene and the second metaphase in meiosis, after which stages, *i.e.*, during an anaphase, it is known as a daughter-chromosome.



- Chromomeres*, the smallest particles identifiable by their characteristic size and position in the chromosome thread.
- Crossing-over*, the exchange of corresponding segments between corresponding chromatids of different chromosomes; a process inferred genetically from the reassociation of linked factors in Mendelian hybrids and cytologically from the reassociation of parts of chromosomes in structural hybrids.
- Deficiency*, loss or "deletion" of a segment of a chromosome from the diploid complement.
- Diakinesis*, the last stage in the prophase of meiosis—immediately before the disappearance of the nuclear membrane.
- Diploid*, (a) the zygotic number of chromosomes ( $2n$ ) as opposed to the gametic or haploid number ( $n$ ); (b) an organism having two sets of chromosomes ( $2\times$ ) as opposed to organisms having one (haploid), three (triploid) or more sets ( $\times$ ,  $3\times$ , etc.).
- Duplication*, the occurrence of one segment of a chromosome twice in the same complement.
- Genome*, a chromosome set.
- Interchange*, an exchange of non-homologous segments of non-homologous chromosomes.
- Inversion*, the reversal of the linear sequence of the genes in one segment of a chromosome relative to an adjoining segment.
- Meiosis*, a form of mitosis in which the nucleus divides twice and the chromosomes once. The prophase of meiosis is the prophase of the first of the two divisions.
- Metaphase*, the stage of mitosis or meiosis in which the chromosomes lie in a plane at right angles to the axis of the spindle and half-way between the poles.
- Pairing of Chromosomes*, the coming together of homologous chromosomes during cell-division.
- Polyloid*, an organism with more than two sets of homologous chromosomes. The terms used are triploid, tetraploid, pentaploid, and so on. Higher multiples are best referred to as  $14\times$ ,  $22\times$  and so on.
- Prophase*, the stage in mitosis or meiosis from the appearance of the chromosomes to metaphase.
- Reduction Division*, formerly applied to the one of the meiotic divisions at which a particular author thought reduction and segregation occurred.
- Rings*, chromosomes associated end to end in a ring, usually by terminal chiasmata.
- Segregation*, the separation of chromosomes of paternal and maternal origin at meiosis and the separation of the differences observed genetically.
- Tetraploid* (v. Polyloid).
- Triploid*, an organism having three sets of chromosomes.
- Univalent*, a body at the first meiotic division corresponding with a single chromosome in the complement; especially when unpaired. Bivalent, Trivalent, etc., are associations of chromosomes held together between diplotene and metaphase of the first division by chiasmata.





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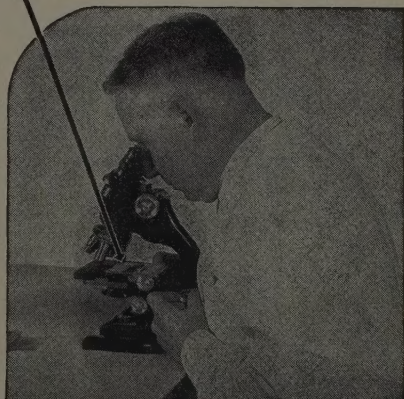
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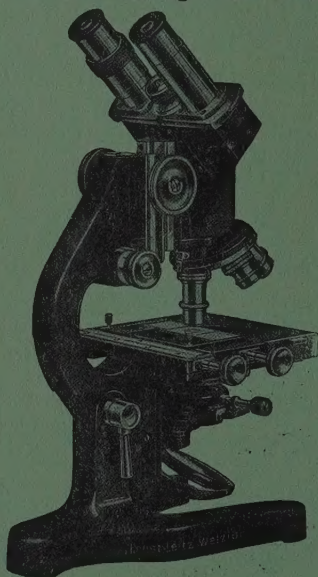
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